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ELECTRO-ORIENTATION IN SHARKS AND RAYS: THEORY AND EXPERIMENTAL EVIDENCE

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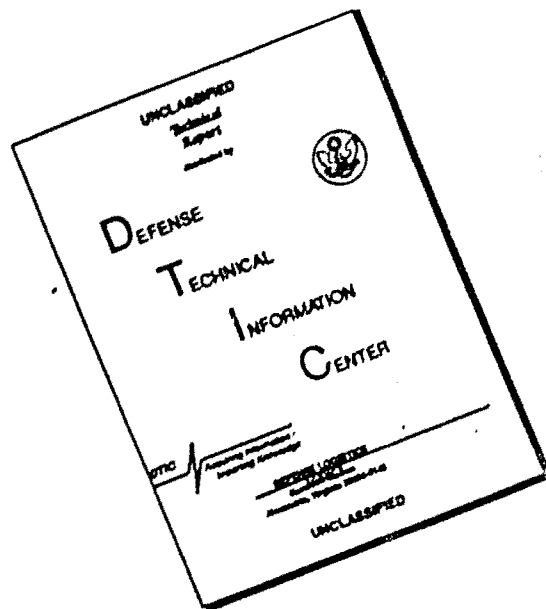
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This paper discusses the hypothesis of electro-orientation in sharks and rays by means of the inanimate motional electric fields occurring in the ocean.

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ELECTRO-ORIENTATION IN SHARKS AND RAYS:

THEORY AND EXPERIMENTAL EVIDENCE

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INTRODUCTION

In previous work (KALMIJN, 1966, 1971, 1972), the author showed
that sharks and rays are able to locate their prey electrically by
taking advantage of the b i o e l e c t r i c fields emanating from
aquatic animals. In the light of these new data, the present paper
discusses the hypothesis of electro-orientation in sharks and rays by
means of the i n a n i m a t e motional electric fields occurring
in the ocean.

Motional electric fields are induced whenever water is moving or
a fish is swimming through the earth's magnetic field (FARADAY, 1832).
In either instance, the motional electric fields may provide electro-
sensitive animals with orientational cues. The nature of these cues
depends on whether the fields are imposed upon the animals (passive
electro-orientation, Fig. 1 A) or result from their own swimming activ-
ity (active electro-orientation, Fig. 1 B). In the passive case, the
motional electric fields may inform drifting animals of the upstream
and downstream directions; in the active case, they may indicate the
actual compass directions north, south, east, and west.

PASSIVE ELECTRO-ORIENTATION

Let us first consider the motional electric field imposed upon animals by a uniform surface stream in an otherwise stationary ocean (cf. LONGUET-HIGGINS et al., 1954). If the stream flows with a velocity $\underline{v}$ through the earth's magnetic field $\underline{B}$, a voltage gradient $\underline{v} \times \underline{B}$ is induced (refer to Fig. 2). This voltage gradient is perpendicular to both $\underline{v}$ and $\underline{B}$, and has a magnitude $vB\sin\alpha$, where α is the angle between $\underline{v}$ and $\underline{B}$. The vector $\underline{v} \times \underline{B}$ represents the motional emf per unit distance. In particular, when the stream crosses the _vertical_ component of the earth's magnetic field $\underline{B}_v$, it induces a _horizontally_ directed voltage gradient $\underline{v} \times \underline{B}_v$. For the electrical detection of passive drift, $\underline{v} \times \underline{B}_v$ forms the principal source of information.

Since the medium is conductive, the induced voltage gradient $\underline{v} \times \underline{B}_v$ gives rise to loop currents through the stationary environment. According to Ohm's Law, these currents develop voltage gradients along their paths. If ρ denotes the resistivity of the water and $\underline{J}$ the electrical current density, the ohmic voltage gradients equal $-\rho\underline{J}$.

The resultant motional electric field $\nabla\phi$, measured with reference to the stationary environment, is given by the vector sum of the induced field $\underline{v} \times \underline{B}_v$ and the ohmic field $-\rho\underline{J}$,

$$\nabla\phi = \underline{v} \times \underline{B}_v - \rho\underline{J}.$$

In this formula, $\underline{v}$, $\underline{B}_v$, and ρ are primarily local characteristics. The current density $\underline{J}$, however, is a function of all $\underline{v}$'s, $\underline{B}_v$'s, and

ρ's in the field, which makes the motional electric fields in natural streams difficult to evaluate.

If a uniform seawater stream is completely insulated from the stationary environment, no current flows and $-\rho \underline{J}$ vanishes, leaving $\nabla \phi = \underline{v} \times \underline{B}_v$. This might be the case where water passes through a narrow channel in high-impedance rock. If, on the other hand, a wide but shallow open-ocean stream is short-circuited by deeper water layers, $-\rho \underline{J}$ is maximal and equals $- \underline{v} \times \underline{B}_v$, i.e. $\nabla \phi = 0$. Consequently, in deep ocean, the actual motional electric fields of surface streams tend to be neglegibly weak.

$\nabla \phi$ may be measured with two stationary electrodes connected to a high-impedance voltmeter (or the physiological equivalent in electro-sensitive fish). With the electrodes at positions P and Q, a distance $\underline{s}$ apart, the voltmeter reads the potential difference

$$\phi_{QP} = \int_P^Q (\underline{v} \times \underline{B}_v - \rho \underline{J}) \cdot d\underline{s} .$$

If, however, the electrodes and voltmeter are drifting with the flow of water, they also are subject to motional electric induction. As they move through the earth's magnetic field with the same velocity $\underline{v}$ as the water, a voltage gradient $\underline{v} \times \underline{B}_v$ is induced in them as well. Provided that the voltmeter does not draw any current, the potential difference generated in the moving measuring system PQ is

$$\int_P^Q (\underline{v} \times \underline{B}_v) \cdot d\underline{s} .$$

Therefore, instead of measuring the actual potential difference in the water, the voltmeter indicates

$$\int_P^Q (\underline{v} \times \underline{B}_v - \rho \underline{J}) \cdot d\underline{s} \quad - \quad \int_P^Q (\underline{v} \times \underline{B}_v) \cdot d\underline{s},$$

which reduces to

$$\int_P^Q -\rho \underline{J} \cdot d\underline{s}.$$

That is, with reference to the moving water, drifting through the earth's magnetic field is electrically identical to being exposed to the ohmic field $-\rho \underline{J}$. Thus, in contrast to stationary systems, a drifting system experiences a minimum field in insulating channels where $-\rho \underline{J}$ tends to zero, and a maximum field in open-ocean streams where $-\rho \underline{J}$ approaches $-\underline{v} \times \underline{B}_v$ (Fig. 2 C).

The vast wind-driven ocean streams, forming a world-wide system of seawater circulations, generate large-scale induction fields, which are virtually uniform to electrosensitive animals. Due to the limited depth of ocean streams (100 - 1000 m) and the heavy loading by deeper water layers, substantial electrical currents are produced. In the Atlantic Ocean, the ohmic voltage gradient $-\rho \underline{J}$, measured with drifting electrodes close to the water surface, ranges from 0.05 to 0.5 $\mu V \cdot cm^{-1}$, corresponding on the average to 90 % of the induced voltage gradient $\underline{v} \times \underline{B}_v$ (VON ARX, 1950, 1962). Because of the great depth of the oceans, the ohmic voltage gradients along the return paths through deeper, stationary water layers must be much weaker. Deep-water flows may complicate the picture, however.

In tidal streams, which are most pronounced along coastlines (especially where narrow channels act as funnels), the flow of water normally extends to the bottom. In the English Channel, the estimated ohmic voltage gradient is $0.25 \, \mu V \cdot cm^{-1}$ when the tidal streams have their maximum velocity (BARBER and LONGUET-HIGGINS, 1948). The return paths for the electrical currents are mainly through the sea bed, which in the English Channel is rather conductive. Therefore, the magnitude of $-\rho \underline{J}$ in the stream still amounts to about 75 % of $\underline{v} \times \underline{B}_v$. A better insulated channel is the St. Croix Estuary between Maine and New Brunswick, where the value of $-\rho \underline{J}$ equals about 16 % of $\underline{v} \times \underline{B}_v$ (TRITES and MacGREGOR, 1962).

What kind of information might the motional electric fields of seawater currents offer to electrosensitive animals? Ideally, sedentary animals in insulated channels are subject to voltage gradients of $\nabla \phi = + \underline{v} \times \underline{B}_v$, whereas drifting specimens in short-circuited ocean streams experience voltage gradients of $-\rho \underline{J} = - \underline{v} \times \underline{B}_v$. Therefore, under favorable circumstances, animals might electrically sense the upstream and downstream directions as well as the speed of the seawater current in which they find themselves.

REGNART (1931) vaguely suggested that FARADAY's motional electric fields "might play some part in deep-sea, and possibly in shore life." DEELDER (1952) more specifically claimed that they could serve as orientational cues during the long-distance migratory journeys of the European eel. The same hypothesis was put forward for the salmon by ROYCE et al. (1968). For sharks and rays, the idea of electro-orientation is quite

conceivable since they are known to show unconditioned cardiac responses to uniform electric fields of voltage gradients as low as $0.01 \mu V.cm^{-1}$ (KALMIJN, 1966). The motional electric fields may be used by animals not only to seek passive transport during migration, but also to compensate for drift and as a basis for orientation during daily excursions. The feasibility of animals orienting in uniform electric fields has recently been demonstrated by KALMIJN and BERNAL (unpublished) who succeeded in training the freshwater electrosensitive fish Sternopygus, when released in the middle of a weak dc field, to turn and swim to the left or to the right depending upon whether the electrical current was either head-on or tail-on. After making a "wrong" turn, the animals were chased to the other side of the experimental tank; after making a "correct" turn, they were left alone until the next trial.

ROMMEL and McCLEAVE (1972) also reported an unexpected sensitivity to low-level electric fields in the American eel, Anguilla rostrata. Eels adjusted to salt water of 40 ohm.cm showed conditioned heartbeat decelerations when tested with dc voltage gradients of $0.067 \mu V.cm^{-1}$, applied in single pulses 5 seconds in duration. The eels responded to fields perpendicular, but not parallel to the body axis, which would enable the animals to align themselves with the direction of the ocean streams they seem to follow during migration. It is questionable, however, whether McCLEAVE's experiments were sufficiently free of stimulus artifacts and polarization effects. Moreover, the eels only responded to transverse stimuli, whereas electric fish are most sensitive just in the longitudinal direction (see BENNETT's critical remarks in McCLEAVE et al., 1971). Lastly, no specific electroreceptors have been described for the eel. Of course, an

electric sense in the eel would be of great biological interest.

Although seawater streams theoretically may be detected by their motional electric fields, even the simplified case of a uniform surface stream in an otherwise stationary ocean has its complications. For instance, an animal in the stationary water lateral to, or under the stream is subject to motional electric fields, though neither the animal nor the water around it are moving. Actually, ocean streams are seldom uniform and the loading by the environment may vary along their course (cf. SANFORD, 1971). Furthermore, surface gravity waves make the top layer of the oceans electrically rather noisy, and other types of electric fields (cf. KALMIJN, 1974) may interfere with the motional electric fields of seawater streams.

In the open ocean, it is mainly the vertical component of the earth's magnetic field that produces the electric fields drifting animals may detect. The voltage gradients induced by broad surface streams crossing the <u>horizontal</u> component of the earth's magnetic field are <u>vertically</u> directed and, due to the water-air interface, usually not sufficiently short-circuited to produce appreciable ohmic voltage gradients (LONGUET-HIGGINS <u>et</u> <u>al</u>., 1954). Therefore, the electrical detection of passive drift in open-ocean streams breaks down towards the magnetic equator where the earth's magnetic field is horizontal in direction.

In summary, electro-orientation by the motional electric fields of ocean streams seems feasible in non-equatorial waters, though even there it is not without limitations.

ACTIVE ELECTRO-ORIENTATION

To discuss _active_ electro-orientation, we next consider a shark _swimming_ in a stationary ocean (Fig. 3). The shark here corresponds to the seawater stream of the former example, and the same motional electric principles apply. If the fish cruises with a velocity $\underline{v}$ through the earth's magnetic field $\underline{B}$, a voltage gradient $\underline{v} \times \underline{B}$ is induced in the animal. As a result, electric currents circulate through the fish and the water around it, causing ohmic voltage gradients $-\rho \underline{J}$ to develop along their paths. Accordingly, the motional electric field of a swimming shark, measured with reference to a stationary observer, is given by

$$\nabla\phi = \underline{v} \times \underline{B} - \rho \underline{J} .$$

Because of its large volume and low resistivity, the seawater practically short-circuits the motional electric field of the fish. Thus, in the animal's skin and body tissues, the _average_ ohmic voltage gradient $-\rho \underline{J}$ largely counteracts the induced voltage gradient $\underline{v} \times \underline{B}$, and the motional electric field $\nabla\phi$ is insignificantly weak. However, the high-resistance electroreceptors _moving_ _with_ _the_ _shark_ do not measure the motional electric field $\nabla\phi$; rather, they detect the average ohmic voltage gradient $-\rho \underline{J}$, which approximates $-\underline{v} \times \underline{B}$ in the heavily loaded animal.

Fig. 3 illustrates the interaction between a shark swimming from the west to the east and the horizontal component of the earth's mag-

netic field $\underline{B}_h$, which in active electro-orientation plays the most important role. The induced voltage gradient $\underline{v} \times \underline{B}_h$ is ventro-dorsally directed. Since $\underline{v} \times \underline{B}_h$ is opposed by the ohmic voltage gradient $-\rho\underline{J}$, the potential difference ϕ_{DV} between the dorsal (D) and ventral (V) surfaces of the animal equals

$$\phi_{DV} = \int_V^D (\underline{v} \times \underline{B}_h - \rho\underline{J}) \cdot d\underline{s} ,$$

with $\underline{s}$ representing any ventro-dorsal path through the body tissues. As a result of the seawater loading,

$$\int_V^D \rho\underline{J} \cdot d\underline{s} \approx \int_V^D (\underline{v} \times \underline{B}_h) \cdot d\underline{s} ,$$

and ϕ_{DV} tends to zero.

Relative to the overall resistivity of the shark's body tissues, the wall of the ampullary electroreceptors offers an extremely high resistance, and virtually no current flows through their jelly-filled canals (WALTMAN, 1966). The jelly is, on the other hand, almost as conductive as seawater (MURRAY and POTTS, 1961). Therefore, the ohmic voltage drop in the ampullary canals must be negligibly weak. Accordingly, the potential buildup along the two ampullary canals depicted in Fig. 3, equals

$$\int_{pore\ 1}^{amp\ 1} (\underline{v} \times \underline{B}_h) \cdot d\underline{s}_1 \quad + \quad \int_{amp\ 2}^{pore\ 2} (\underline{v} \times \underline{B}_h) \cdot d\underline{s}_2 .$$

Since the dorsal and ventral skin pores are nearly equipotential, the greater part of the potential buildup along the ampullary canals develops across the sensory epithelia lining the terminal ampullae of the electroreceptors. In this way, $\underline{v} \times \underline{B}_h$ might be detected by the shark.

The information in motional electric fields of fish may easily be recognized (cf. Fig. 3 C). Through interaction with the horizontal component of the geomagnetic field, the dorsal ampullae become <u>positive</u> with respect to the ventral ampullae when the shark swims <u>westwards</u>; the dorsal ampullae become <u>negative</u> with respect to the ventral ampullae when the shark swims <u>eastwards</u>; and no potential differences are induced when the animal swims either to the north or to the south, i.e. parallel to the magnetic field lines. If the shark is able to evaluate these potential differences, it may use them as a physical basis for a true compass sense. Interaction between the animal and the vertical component of the earth's magnetic field $\underline{B}_v$ induces similar potential differences in the horizontally directed ampullary canals. With this additional information, the shark might sense the inclination of the earth's magnetic field, and thus the latitude of its position on the globe.

In his "Experimental Researches on Electricity," FARADAY (1832) not only anticipated the vast motional electric fields of seawater streams, but also predicted the local electric fields induced by ships crossing the ocean. THORNTON (1931) applied the idea to deep-sea fish and suggested that they "perceive their prey or avoid capture" by the electric fields animals produce when moving in the earth's magnetic field. MURRAY (1962) remarked that sharks and rays, if sensitive enough, might utilize

their own motional electric fields to sense the compass direction in which they swim. At a cruising speed of 100 $cm \cdot s^{-1}$, the vertical component of the induced voltage gradient may be as high as $0.4 \mu V \cdot cm^{-1}$, which is well within the sensitivity range of these animals (KALMIJN, 1966). Moreover, sharks exhibit behavioral responses when swimming into imposed magnetic fields of earth's magnetic field strength (KALMIJN, unpublished). Recently, BRANOVER et al. (1971) reported that the European eel, Anguilla anguilla, showed a statistically distinct bias in a certain compass direction when tested in a hexagonal maze offering many 120° Y choices, whereas their o-rientation became random after the geomagnetic field was neutralized with Helmholz coils. The authors favored a motional electric detection of the earth's magnetic field, but they failed to produce convincing evidence. Alternatively, compass orientation could also be explained by a direct magnetic detection, as is considered the more plausible mechanism in bees (LINDAUER and MARTIN, 1968, 1972) and in birds (KEETON, 1972).

One complication in active electro-orientation should be mentioned. When a shark swims forwards, the water it displaces turns backwards, in-ducing voltage gradients opposing those of the animal itself. However, this effect probably does not weaken the electrical stimulus to the fish more than a few percent (T.B. SANFORD, pers. comm.). The vortices shed off by the animal's tail seem to be even less disturbing.

Since active electro-orientation mainly depends on the horizontal component of the earth's magnetic field, an animal would obtain the strongest pertinent signals when swimming near the magnetic equator. In contrast, the higher magnetic latitudes are more favorable for the detec-tion of passive drift (see above).

The active system has an advantage over the passive system in being less affected by interfering electric fields, for an animal may voluntarily control its own motional electric field by varying either speed or direction of swimming. In the same way, the animal may discriminate between the activily and passivily induced electric fields, i.e. the two electro-orientation systems may operate side by side. The stimulus to an animal swimming in a stream may be found by vectorially adding the effects of (1) drifting relative to the stationary environment, and (2) swimming relative to the water in the stream.

A problem touching both types of electro-orientation is the geological variance in the earth's magnetic field. Since Precambrian times, several -- on a kiloyear scale -- sudden reversals of the earth's magnetic field have supposedly taken place, though the field strength during the reversals probably did not fall below 10 - 20 % of its normal value (cf. BULLARD, 1968).

The theory of electro-orientation by motional electric fields has intentionally been illustrated with marine examples only, since (1) other fields not resulting from motional electric induction seem to prevail in the freshwater habitat, and (2) freshwater fish are probably 10 to 100 times less sensitive to low-frequency voltage gradients than marine sharks and rays (cf. KALMIJN, 1974).

This discussion on passive and active electro-orientation suggests -- but does not imply -- that motional electric fields play a role in the animal's life. Further experimentation will be required to settle the question.

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Note:

A more complete treatise on electric fields and their significance to electrosensitive animals will be published in the Handbook of Sensory Physiology, Volume III/3, A. Fessard, ed. Springer - Verlag: Berlin - Heidelberg - New York (in the press).

Flow of water

Induced electric
current

Vertical component of
earth's magnetic field

Fish drifting in
shallow ocean stream

Fig. 1 A.

Induced electric current

Horizontal component of earth's magnetic field
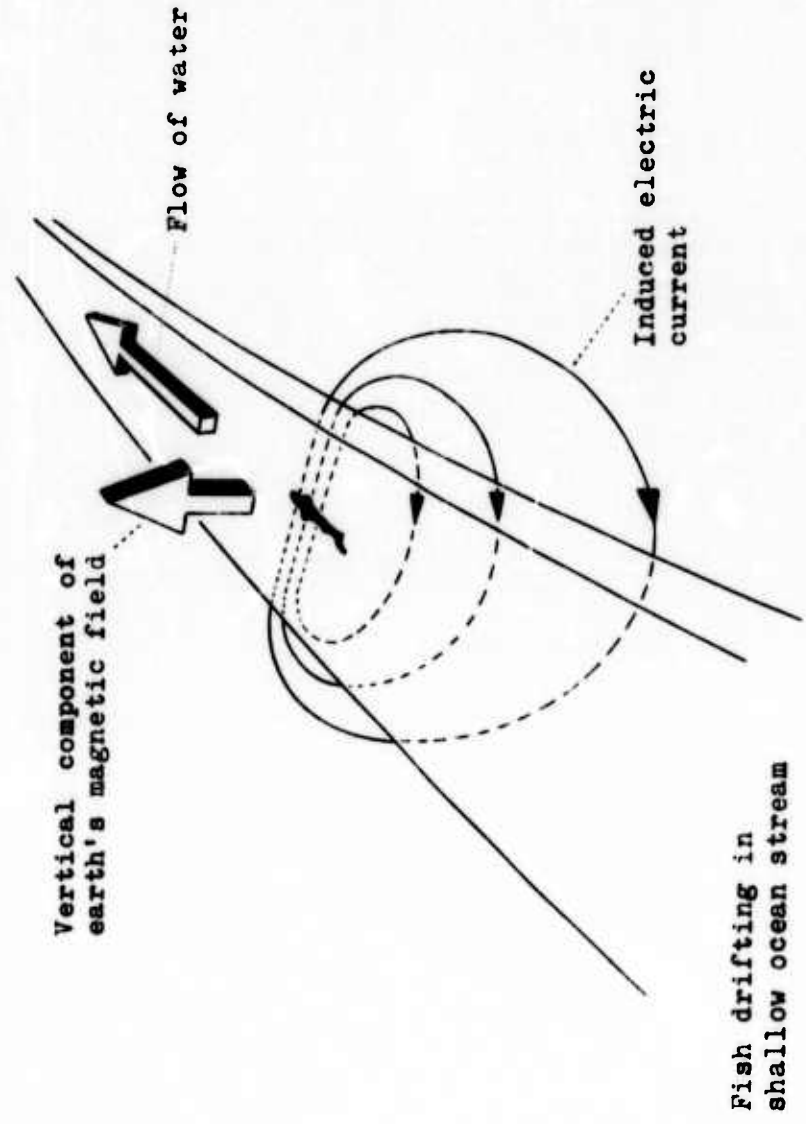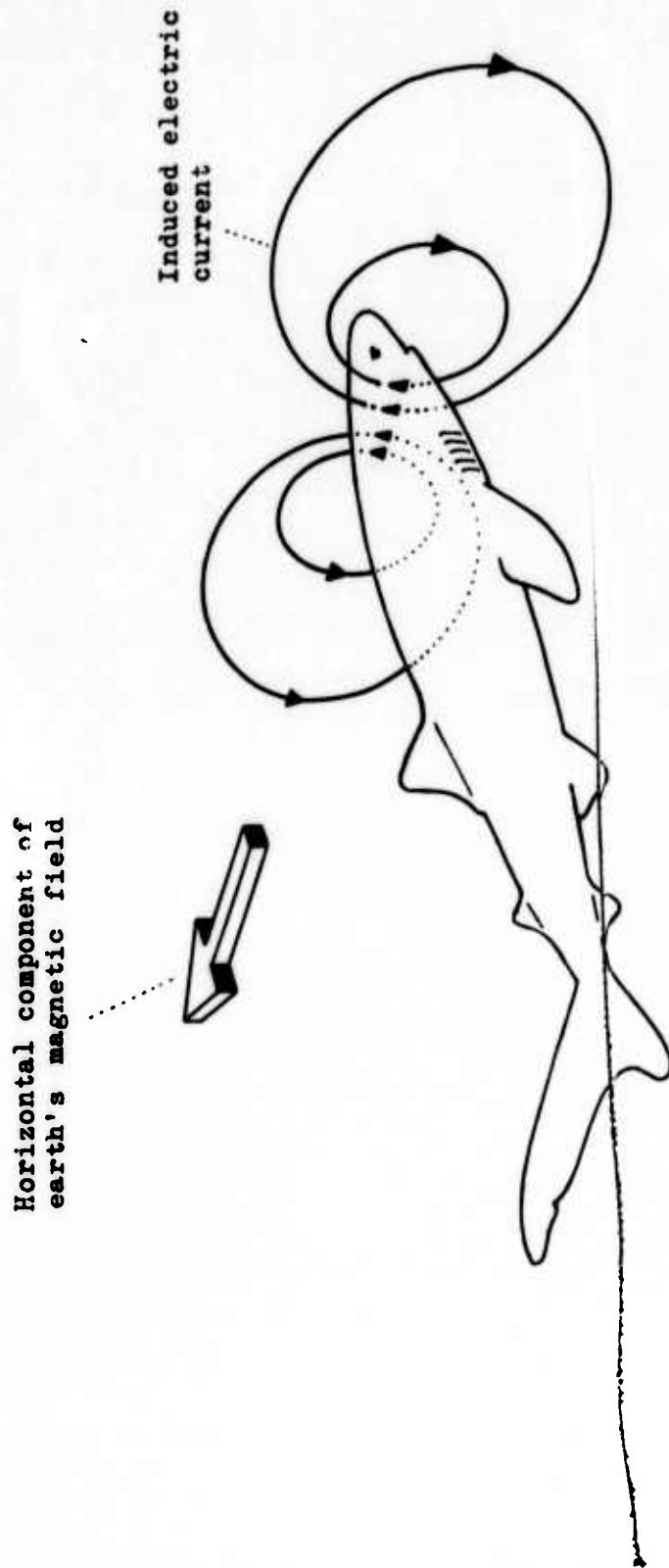
Fish swimming in stationary ocean

Fig. 1 B.

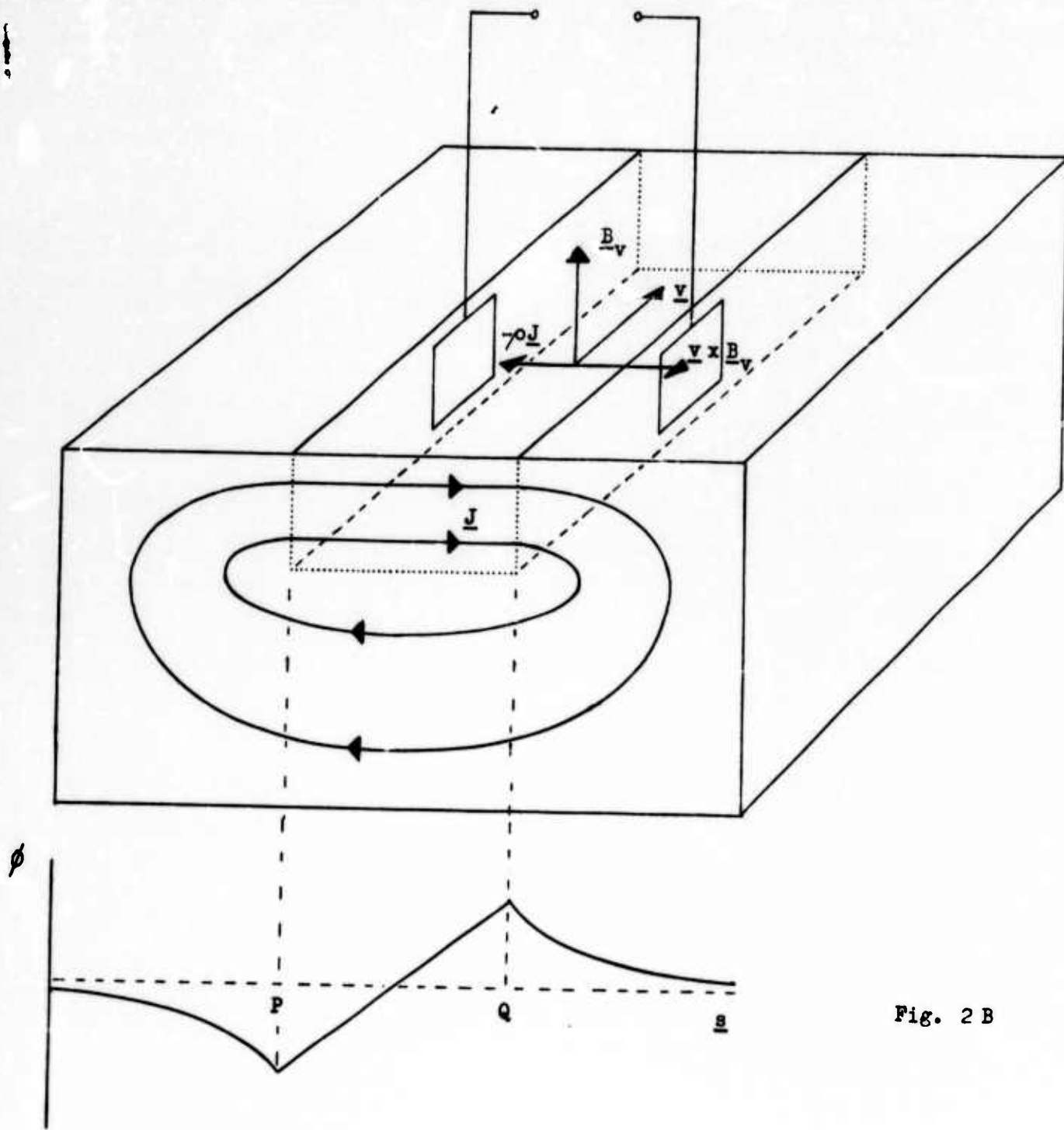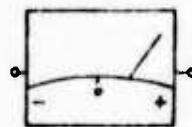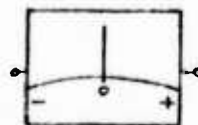measuring system

Fig. 2 A   a. stationary   b. drifting

Fig. 2 B

Fig. 2 C

Insulated stream, $\rho \underline{J} = 0$, stationary electrodes, voltmeter indicates:
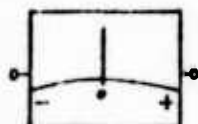
$$\underline{v} \times \underline{B}_v$$

Insulated stream, $\rho \underline{J} = 0$, drifting electrodes, voltmeter indicates:

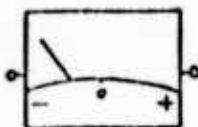$$(\underline{v} \times \underline{B}_v)_{stream} - (\underline{v} \times \underline{B}_v)_{meter} = 0$$

Short-circuited stream, $\rho \underline{J} = \underline{v} \times \underline{B}_v$, stationary electrodes, voltmeter indicates:

$$\underline{v} \times \underline{B}_v - \rho \underline{J} = 0$$

Short-circuited stream, $\rho \underline{J} = \underline{v} \times \underline{B}_v$, drifting electrodes, voltmeter indicates:

$$(\underline{v} \times \underline{B}_v - \rho \underline{J})_{stream} - (\underline{v} \times \underline{B}_v)_{meter} = -\rho \underline{J}$$

Legend

Fig. 2. A. Seawater stream in otherwise stationary ocean. $\underline{B}_v$, vertical component of earth's magnetic field; $\underline{v}$, velocity of stream; $\underline{v} \times \underline{B}_v$, induced voltage gradient; $\underline{J}$, current density; $-\rho \underline{J}$, ohmic voltage gradient. The stream is moderately loaded, $\rho \underline{J} < \underline{v} \times \underline{B}_v$. In a. the measuring system is stationary, indicating $\nabla \phi = \underline{v} \times \underline{B}_v - \rho \underline{J}$; in b. the measuring system is drifting, indicating $-\rho \underline{J}$. B. Potential distribution ϕ along the electrode axis $\underline{s}$. C. Summary of voltage gradients indicated by measuring system under four extreme conditions discussed in the text.
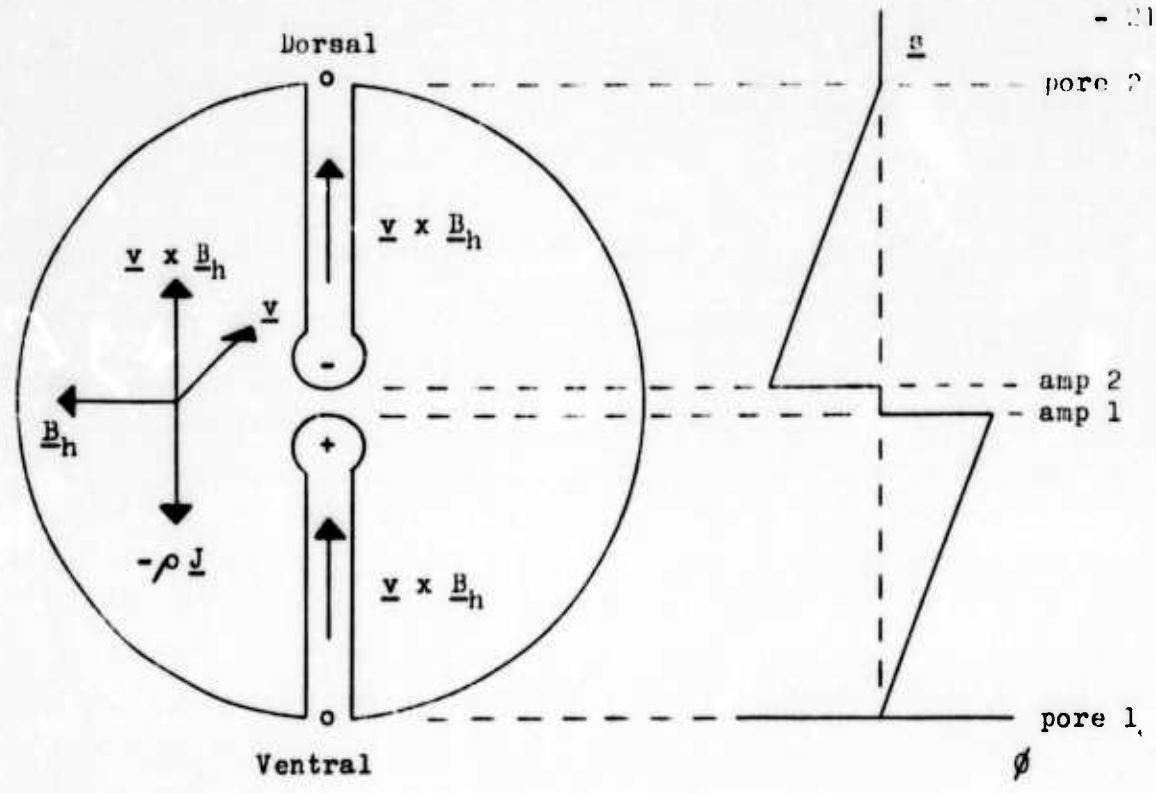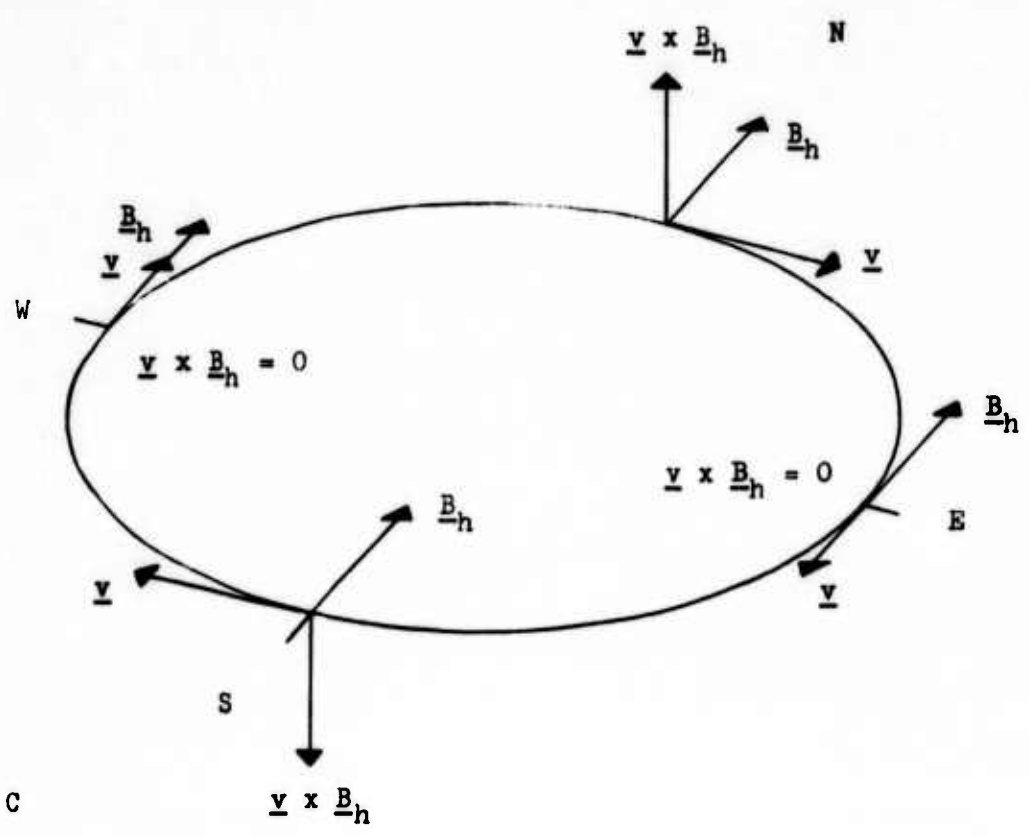
Fig. 3

A

B

Fig. 3 C

Legend

Fig. 3. A. Cross-section of shark swimming through earth's magnetic field in west-east direction. $\underline{B}_h$, horizontal component of earth's magnetic field; $\underline{v}$, velocity of shark; $\underline{v} \times \underline{B}_h$, induced voltage gradient; $-\rho \underline{J}$, ohmic voltage gradient. The shark is almost short-circuited, $\rho \underline{J} \approx \underline{v} \times \underline{B}_h$ and $\phi_{DV} \approx 0$. B. Potential distribution along ampullary axes $\underline{s}$. C. Successive situations for shark circling through compass directions.